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2. When an alternative exists at the cut end we meet with the problem of polarity also. In the hydroid, *Tubularia*, an analysis of the conditions leads me to conclude: (1) That the hypothesis of stuffs moving in given directions does not explain the facts, (2) that the results can be accounted for on the ground of the amount of nutritive substance present in the pieces, taken in connection with the relative conditions of the stem at each level. Furthermore, in this case the stimulus of the water on the exposed end, calling forth hydranth regeneration, is an important factor in the result.

3. There is nothing in the phenomena to suggest that the old part has a stereometric influence, *i. e.*, a directive influence on the new part, as the term 'polarity' suggests. On the contrary, the influence is largely centripetal in direction, so far as there is any question of direction involved.

4. An analysis of the conditions present in lateral regeneration in planarians suggests that at least three separate factors are to be recognized in the changes that take place. I have put these factors into the categories of (a) totipotency, (b) heterotopy and (c) organization.

5. The ends of the old organs have also an influence on the regeneration, but a less important one in some cases than those just mentioned.

6. The same factors are also present in antero-posterior regeneration in which an alternative is present. When *no* alternative exists the totipotency has certain limitations, which depends, however, on the special combination of tissues in the new part, rather than on any limitations in each group of cells.

7. The organizing principle acts on the new and old part *as a whole* and determines the relative arrangement and proportions of the new organs.

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#### MOSAIC DEVELOPMENT IN THE ANNELID EGG.\*

OUR general interpretation of the problem of development has been somewhat prejudiced by the fact that so much of the earlier experimental work dealt with such eggs as those of echinoderms, medusæ, *Amphioxus* or the nemertines, where any one of the first two or four cells may produce a perfect dwarf embryo; for such cases seem at first sight to be irreconcilably opposed to any theory of definite pre-localization or mosaic development. The collapse of the Roux-Weismann theory of differentiation by qualitative nuclear division discredited for a time the whole mosaic theory; but more recent experimental work, especially on the eggs of ctenophores and mollusks, promises to re-establish it on a new basis. In the course of the past year I have been able to show experimentally that the development of mollusks (*Dentalium*, *Patella*) conforms in its main features to the mosaic principle, and, furthermore, that the cleavage mosaic is foreshadowed by a very definite original pre-localization of specific protoplasmic materials in the undivided egg. During the past summer I have had an opportunity to extend these observations in some measure to the egg of an annelid, where the same general principle has been found to hold true.

The development of the annelids presents the problem in a very clear-cut form, since from the first cleavage onward the principal material of the segmented trunk-region lies in the posterior cell of the embryo, and this cell is in most species somewhat larger than the anterior, and hence may be immediately identified. The experiments here reported consist in a comparison of the development of the isolated posterior cell of the two-cell stage with

\* Read before the National Academy of Sciences, November 16, 1904.

that of the isolated anterior cell, especially in the genus *Lanice*, which I have found the most favorable egg for operation of all the many forms tested. While the number of successful operations has been rather small, they have given a very definite result, and one that is in its main features in agreement with the one earlier obtained in the eggs of the mollusk *Dentalium*. When either cell of the two-cell stage is destroyed, the remaining cell segments as if it still formed a part of an entire embryo. The later development of the two cells differs in an essential respect, and in accordance with what we should expect from a study of the normal development. The posterior cell develops into a segmented larva with a prototroch, an asymmetrical pre-trochal or head region, and a nearly typical metameric seta-bearing trunk region, the active movements of which show that the muscles are normally developed. The pre-trochal or head-region bears an apical organ, but is more or less asymmetrical, and, in every case observed, but a single eye was present, whereas the normal larva has two symmetrically placed eyes. The development of the anterior cell contrasts sharply with that of the posterior. This embryo likewise produces a prototroch and a pre-trochal region, with an apical organ, but produces no post-trochal region, develops no trunk or setæ, and does not become metameric. Except for the presence of an apical organ, these anterior embryos are similar in their general features to the corresponding ones obtained in *Dentalium*. None of the individuals observed developed a definite eye, though one of them bore a somewhat vague pigment spot.

This result shows that from the beginning of development the material for the trunk region is mainly localized in the posterior cell; and, furthermore, that this material is essential for the development of the

metameric structure. The development of this animal is, therefore, to this extent at least, a mosaic-work from the first cleavage onward—a result that is exactly parallel to that which I earlier reached in *Dentalium*, where I was able to show that the posterior cell contains the material for the mesoblast, the foot and the shell; while the anterior cell lacks this material. I did not succeed in determining whether, as in *Dentalium*, this early localization in *Lanice* preexists in the unsegmented egg. The fact that the larva from the posterior cell develops but a single eye suggests the possibility that each of the first two cells may be already specified for the formation of one eye; but this interpretation remains doubtful from the fact that the larva from the anterior cell did not, in the five or six cases observed, produce any eye. This subject remains for further examination, which I hope to be able to carry out hereafter.

These observations, in connection with my preceding ones on the molluscan egg, contribute to the growing body of evidence that the development both of annelids and of mollusks is to be regarded as a mosaic-work of self-differentiating cells; and, further, that the specific morphogenic factors are connected in some way with specific forms of protoplasm, which I think may conveniently be designated as formative (perhaps better, 'morphoplasmic') stuffs. I have endeavored in two recently published papers to show that the same principle applies to the eggs of other animals, even in such cases as the sea-urchins or *Amphioxus*, where either of the first two cells may produce a complete embryo. The explanation of the difference between the two cases appears to be that in the mollusk or annelid the cytoplasmic stuffs undergo an asymmetrical distribution during the first division, while in the sea-urchin or *Amphioxus* the distribution is symmetrical. The division is, therefore, in the first case

qualitative, in the second case quantitative only, thus giving the immediate possibility of the production of two embryos from a single egg. It appears to me that we find here a principle of reconciliation between the hypothesis of mosaic development and pre-localization, and the apparently contradictory one of non-mosaic or correlative differentiation. The facts show that each of these apparently contradictory hypotheses contains an element of truth; that we must recognize in the development of every animal the fact of pre-localization and of mosaic development, but also the fact of correlative action. The relation between these two can not be predicted, but must be determined in each individual case; for the known facts are already sufficient to prove that the segregation of the formative stuffs is a process that occurs at different periods in different animals. At the time of fertilization, accordingly, the segregation differs both in degree and in form; and these differences have not yet been reduced to any general law.

In conclusion, I would express the opinion that, so far as the early stages of development are concerned, it is difficult to escape the hypothesis of formative stuffs or specific morphoplasmic substances, in some form. But while this hypothesis facilitates an understanding of the *modus operandi* or immediate causes of differentiation, it leaves us as much as ever in the dark as to the localizing or form-determining factors which are responsible for the determination of the segregation pattern. This problem, which is essentially one of correlative action, is not only unsolved, but suggests the existence of specific energies for which it is difficult at present to find an analogy outside the field of protoplasmic action.

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#### SCIENTIFIC BOOKS.

*Contributions to the Study of the Behavior of Lower Organisms.* By HERBERT S. JENNINGS. Published by the Carnegie Institution of Washington. 1904. 256 pp., 81 text-figures.

In the series of papers which make up this volume Professor Jennings presents results which are of fundamental importance for our understanding of the behavior of lower organisms. The titles of the seven papers of the volume are as follows: (1) 'Reactions to Heat and Cold in the Ciliate Infusoria,' (2) 'Reactions to Light in Ciliates and Flagellates,' (3) 'Reactions to Stimuli in Certain Rotifera,' (4) 'The Theory of Tropisms,' (5) 'Physiological States as Determining Factors in the Behavior of Lower Organisms,' (6) 'The Movements and Reactions of Amœba,' (7) 'The Method of Trial and Error in the Behavior of Lower Organisms.'

For the purposes of this review the papers may be separated into three groups. Of these the first, which includes the first three papers, is devoted primarily to descriptions of the modes of reaction of several of the lower organisms, and to a discussion of the bearing of these reactions upon the 'orientation theories' of Loeb and Verworn. The second group is constituted by the paper on Amœba; in it the author deals in detail, as a result of his own observation, with the mechanics of locomotion, modes of reaction and psycho-physiology of the organism. Papers four, five and seven are included in the third group. In addition to presenting several points of interpretation, they contain discussions of the relations of the author's results to the general theory of tropisms.

I shall now attempt to state briefly the principal points made in each of these three subject divisions of the volume.

In explanation of the directive influence of stimuli on the movements of various organisms Loeb, Verworn and others have proposed the so-called orientation theories.

According to these theories a stimulus which acts unequally upon different portions of the body causes inequality of contraction in the musculature, and thus brings about a turning